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"The Effects of Luminance Boundaries on Color Perception"

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15 November 1989

A. Abstract

When a suprathreshold luminance flash, presented as an increment on a larger background field, accompanies a circular isoluminant chromatic flash at the same spatial location, chromatic threshold is reduced by about two-fold. This facilitation results from the clearly-visble edges of the luminance flash (the "pedestal") serving to demarcate the test region, segregating it from its surround. Recent signal detection experiments show that this facilitation does not occur as a result of the contour's reducing the spatio-temporal detection uncertainty of the observer; instead of merely directing the observer's attention, the pedestal must alter the properties of chromatic detectors (by changing the extent of spatial integration, for instance). A thin luminance ring can be used to create the facilitating contour. Displacing the ring relative to the test causes the facilitation to decline sharply, as if the visual system integrated uniformly within the demarcated region. However, the contour does not have to enclose the test region: small segments of the ring presented on the test circumference have about half the maximum facilitatory effect, while 180 deg of arc produces the whole effect. These results can be used as a rigorous means of probing the way in which low-level visual attributes (edges, color) interact at higher levels.

A further set of studies examined pathways that receive signals from short-wavelength, S, cones. It had been thought that S cones only contributed to color, but we have demonstrated S-cone input into both luminance and chromatic pathways. In all pathways, S cone signals oppose those from the middle-wavelength cones.

B. Background

Visual perception is concerned with the recognition of objects. Objects are made up of surfaces, and surfaces are bounded by edges. The goal of this research program is to understand better the ways in which edge or boundary information, carried primarily by the luminance system, interacts with chromatic information to determine the color of a region of the visual field. Much recent evidence from physiology (e.g., Maunsell & Newsome, 1987) indicates that different kinds of information are processed at early stages in separate, parallel streams in the brain. However, visual perception is unitary: we perceive objects, not disembodied properties such as luminance and color, suggesting that the separate streams must interact at higher stages within the visual system.

In the study of machine vision, some success has been achieved in understanding low-level visual "modules" (such as edge detectors and color estimation algorithms) from the computational perspective. Recent efforts have focussed on ways in which these low-level modules can interact and generate unified representations of the visual input (e.g., Poggio, et al. 1988). Our research can be viewed as a psychophysical investigation of these same interactions. By presenting weak color stimuli (which have no visible edges) together with suprathreshold luminance stimuli (which have edges), we can independently manipulate the surface attribute and the edge, and study their interaction.

It has long been observed that luminance edges affect suprathreshold chromatic perception, influencing spatial segregation and filling-in of color. We have been studying how luminance contours affect chromatic detection--a *threshold* process. Contour information provided by the higher resolution luminance system can facilitate chromatic detection. The studies reviewed here and our work (next section) provide strong evidence for such facilitation.

Hilz and Cavonius (1970) and Hilz et al. (1974) showed that wavelength discrimination measured with square-wave gratings (interlaced bars of two different spectral wavelengths) was improved when the adjacent bars were of slightly different luminance. Similar effects were observed with a spot stimulus (ca. 560 nm) on a large uniform field. Chromatic discrimination may thus be improved by a spatially-coincident luminance pattern. The chromatic facilitation by the coincident pattern, or pedestal, increased as the spot was reduced from 34.8' to 3.6' or as the grating was increased in spatial frequency from 2.4 to 7.2 c/deg (Hilz et al.). The results were striking for the spot stimuli: the chromatic threshold was 20x higher for the smallest spot compared to the the largest spot when no luminance pedestal was present (isoluminant condition); when a luminance pedestal of 5% contrast was present, the chromatic thresholds for all spots dropped to an approximately *constant low* value. Thus chromatic detection appears not to be penalized for small size when a luminance pedestal is concurrently present. We are attempting to replicate this important result with our better apparatus and method, in on-going experiments.

The luminance pattern might serve to delineate the chromatic test region, permitting a better comparison of the color of the test with the surround. This hypothesis was examined by Boynton et al. (1977) in their study of the Gap effect. They hypothesized, "Hue has a tendency to fill in uniformly between contours....It is proposed that there exists some kind of averaging mechanism that assigns only one mean value for the hue of a region, rather than many point-for-point values." By inserting a 2.7' wide dark gap between two precisely juxtaposed, isoluminant fields, they found improved chromatic discrimination when the two half-fields differentially stimulated only S cones. The gap also improved discrimination mediated by the difference of M and L cone signals, but only when the field was reduced somewhat in size. Nick and Larimer (1983) obtained similar effects with an S-cone-detected flash presented on a suprathreshold, coincident yellow luminance pedestal on a large yellow field. Eskew (1989; enclosed) has shown that an equiluminant suprathreshold chromatic gap can also produce the gap effect (see section C7).

The goals of this research project include: (1) Measurements of the spatial and temporal properties of the facilitation process. For instance, how is facilitation affected when the contour and the equiluminant spot are displaced in time or space, relative to one another? Sections C2, C3, and C5 discuss results. (2) To study how the statistics of the chromatic detection process might be altered by the contour. In particular, why does the contour linearize detection (Section C2)? Is this due to a reduction in detection uncertainty? Section C4 rejects this explanation. (3) To understand what types of contours will produce facilitation. For instance, will suprathreshold equiluminant contours interact with chromatic mechanisms the same way luminance contours do? Sections C2 and C7 provide partial answers. (4) To study the temporal properties of the red-green opponent mechanism. Section D discusses fundamental results. (5) To understand the ways in which short-wave cones contribute to luminance and color. Section E gives an overview.

C. Summary of Research on Color-Contour Interactions

1. Method

Our stimuli are > 520 nm and thus we need consider only the M and L cones. Stromeyer *et al.* (1985) and Eskew *et al.* (1989a) show that the Smith and Pokorny (1975) cone fundamentals adequately represent our observers.

We represent stimuli in normalized cone quantal catch coordinates. The vertical axis indicates the change (ΔM) in the M cone catch owing to the test, normalized by the M cone catch owing to the adapting field, and the horizontal axis represents the same variable for L cones. Electrophysiology shows that the cones adapt and obey Weber's law (Normann and Perlman, 1979), and thus the Weberian coordinates take into account the differential adaptation of the M and L cones caused by the adapting field. The coordinates represent *stimulus* magnitudes *per se*: the test contrast 'seen' by each class of cones.

The local Weberian representation that we use may be contrasted with the "cardinal axes" space of Krauskopf et al. (1982). While these "cardinal axes" represent any stimulus in three linearly independent axes, the scaling of the coordinates is to a large extent arbitrary. (In fact, unit distances are defined with reference to the amount of light variation that the stimulating apparatus can produce.) This arbitrariness makes comparison of different experiments very difficult. Our Weberian coordinates make comparison of experiments inherently simple and avoid any questions of absolute cone sensitivities. Moreover, by accounting for the known Weberian properties of the cones within the coordinate definitions, our representation directs attention to post-receptoral function.

With our apparatus, we can produce test vectors of all orientations in the Weberian coordinates, allowing us to measure a complete detection contour. The shape of the contour reveals separate luminance and chromatic mechanisms, defined below. The test consists of coincident, simultaneous incremental and decremental flashes of green and red lights. The stimulus (Fig. 1) is created by red, green and yellow 1 deg test regions, and contiguous surrounding 5 deg annuli of the same spectral composition as the tests, all superposed on an intense uniform adapting field. Stimuli are monochromatic (HBW 10-nm), generated with an 8-channel Maxwellian view under computer control. Positive flashes are achieved by increasing the light in the test region (produced with LEDs) above the level of its annular surround, and negative flashes are achieved by decrementing the light. The threshold for the test vector is measured by fixing the vector angle and varying the vector length with a two temporal interval forced-choice (2AFC) paradigm. The thin edge between the 1° test and the surround is not visible, so that between trials the field looks uniform except for the two fixation dots (Fig. 2A).

Our measured detection contours demonstrate luminance and chromatic mechanisms (Stromeyer et al., 1985, 1987). Fig. 3 shows a hypothetical detection contour (thresholds for various

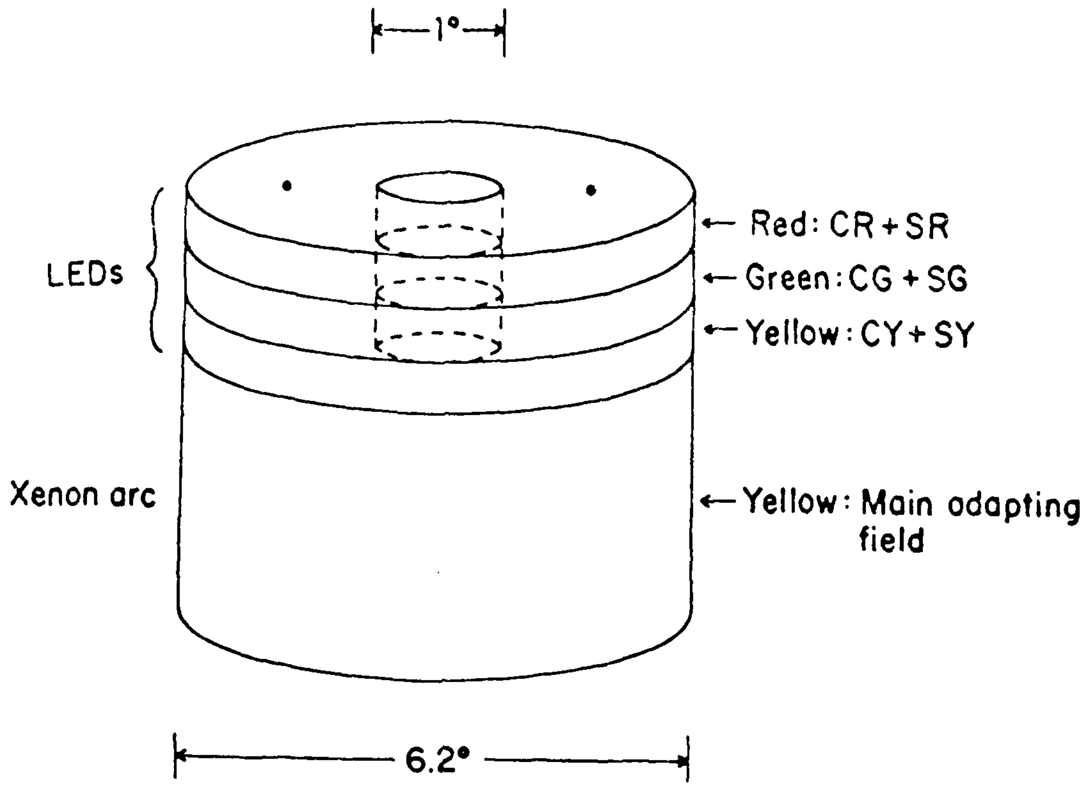

Fig. 1 The components of the stimulus.

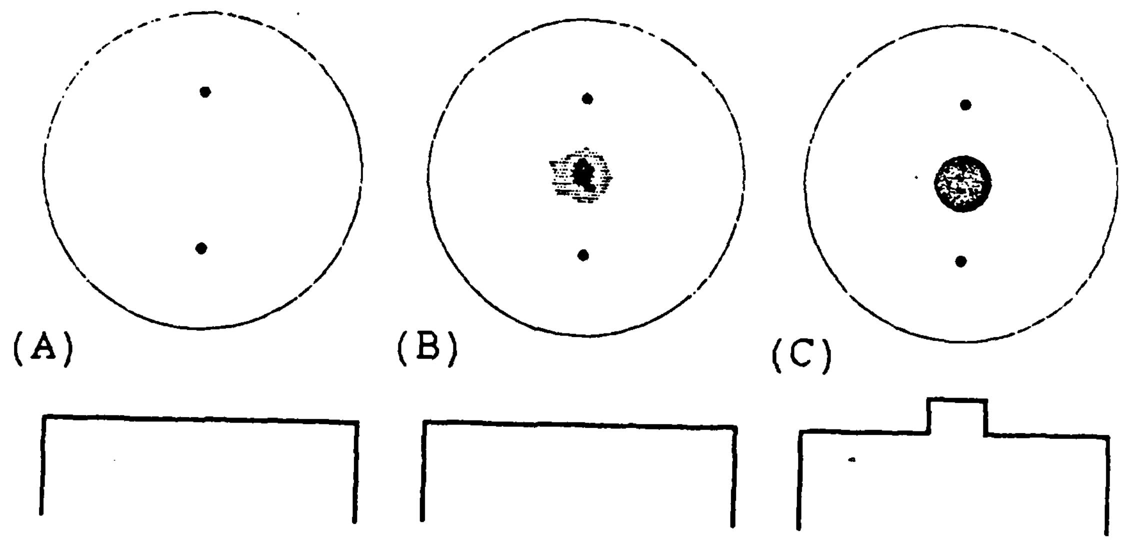

Fig. 2 Appearance of the stimulus and its luminance profile (A) between trials, (B) with an equiluminant test, and (C) with an equiluminant test plus a luminance pedestal.

directions in $\Delta L/L$, $\Delta M/M$ space), and shows how linear segments in the contour define detection mechanisms. The sensitivity of the chromatic mechanism (Stromeyer et al., 1985) is maximal on a chromatically-neutral yellowish field, declines slightly on greenish fields, and declines strongly on reddish fields. We use a yellow field to measure interactions of luminance and chromatic mechanisms.

2. Basic Facilitation Results.

Four basic flashes were used for 'pedestals' (defined below) and tests: positive and negative luminance flashes of 580 nm light (vectors of 45° and 225° in the Weberian coordinates) and positive ('green') and negative ('red') *isoluminant* chromatic flashes (+chromatic and -chromatic, 135° and 315°). The magnitudes of tests and pedestals are represented by their vector lengths, $[(\Delta M/M)^2 + (\Delta L/L)^2]^{1/2}$; this vector length metric is used in all of our work.

An identical 'pedestal' flash was presented in *both* intervals of each 2AFC trial; the test was superposed on the pedestal in one interval. Thus the observer was required to *discriminate* between pedestal and pedestal+test. Each datum point is based on ~4 runs of 150-200 trials. We measured the magnitude of the test threshold as a function of the pedestal intensity, as in the usual masking paradigm (Nachmias and Sansbury, 1974) using all combinations of ±luminance

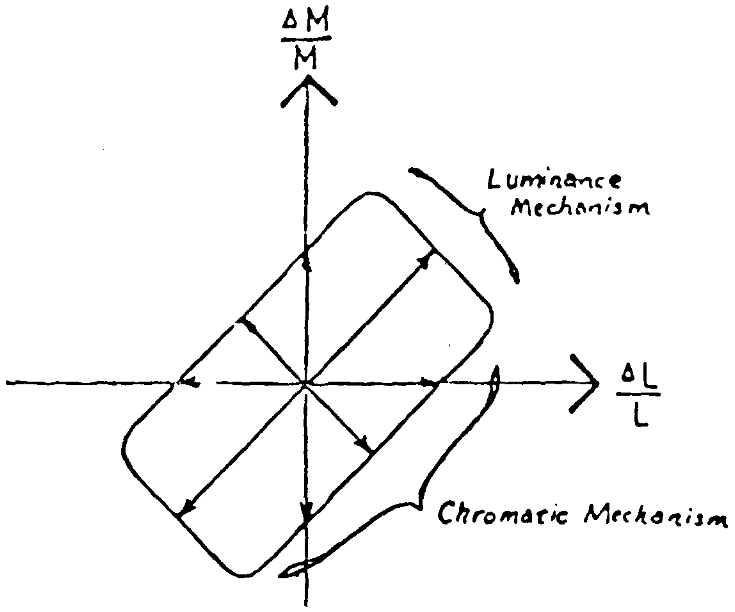

Fig. 3 Hypothetical chromatic detection contour. Linear combinations of cone contrasts form linear segments in the contour and operationally define detection mechanisms.

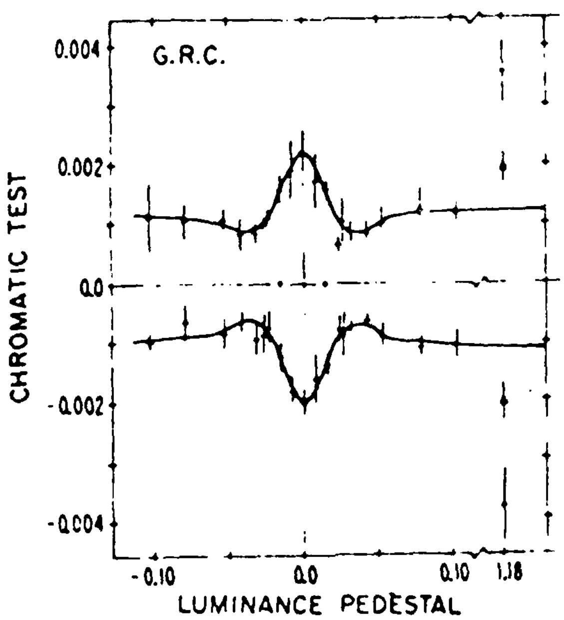

Fig. 4 Chromatic detection thresholds for green (top) and red (bottom) tests, as a function of the incremental (right, positive values) and decremental (left, negative values) intensity of a luminance pedestal. The pedestal facilitates, independent of suprathreshold intensity or polarity.

(i.e.+luminance and -luminance) and ±chromatic test and pedestal flashes. More than 300,000 forced-choice trials were collected (Cole *et al.*, 1990).

CHROMATIC DETECTION ON LUMINANCE PEDESTALS. On the vertical axis of Fig. 4, the intensity of the +chromatic (green) tests is plotted above the horizontal midline, and -chromatic (red) below, while on the horizontal axis, the intensity of +luminance pedestals is plotted to the right of the vertical midline and -luminance to the left. The luminance pedestal has little effect on the chromatic threshold until the pedestal approaches its threshold (indicated by crosses on horizontal midline). As the pedestal is raised to 2-3x threshold, the chromatic threshold descends 2-3x. This facilitation is symmetric: ±luminance pedestals about equally facilitate ±chromatic tests. Remarkably, masking does not occur for extremely intense pedestals of even 100x threshold. We also observed that with the roles of test and pedestal reversed, suprathreshold ±chromatic pedestals weakly facilitated detection of ±luminance tests, and relatively intense chromatic pedestals of 20-30x threshold did not produce luminance masking. (The luminance test often appeared to change the saturation of the chromatic pedestal.)

CHROMATIC IDENTIFICATION ON LUMINANCE PEDESTALS. The subjective result of facilitation is striking. The chromatic test at threshold on a uniform field appears as a highly diffuse tinge of color (Fig. 2B). When the green or red test is set just below threshold and then a suprathreshold yellow luminance pedestal is added, the sharply delineated pedestal looks decidedly green or red and approximately uniformly colored owing to the chromatic test (Fig. 2C). We showed that the luminance pedestal equally facilitates the observer's ability to detect the chromatic flash and to identify its sign (red or green).

NONMIXED PEDESTALS AND TESTS. The threshold curves for chromatic tests (Fig. 4), showed that subthreshold luminance pedestals had little effect and intense pedestals produced facilitation. Experiments were repeated with *both* pedestal and test as luminance stimuli or both as chromatic stimuli. Results were quite similar for the two conditions. Fig. 5 shows results obtained with the chromatic stimuli. The threshold of the chromatic test varies strongly with the chromatic pedestal intensity. Subthreshold pedestals of the same sign as the test produce facilitation and pedestals of the opposite sign produce cancellation. Thus the curves are highly asymmetric about zero pedestal intensity. This is an example of the familiar 'dipper' function, reflecting a strong threshold nonlinearity that is consistent with an accelerated psychometric function (Nachmias and Sansbury, 1974). We measured an acelerated psychometric function (log d' vs log test intensity) for the chromatic test on the uniform field, having a slope exponent of ~2.

LUMINANCE PEDESTAL LINEARIZES SUBTHRESHOLD CHROMATIC RESPONSE. We attempted to remeasure the chromatic dipper function in the above experiment, with the only difference being that a luminance pedestal of 2.1x threshold was also present. The total pedestal (+luminance and +chromatic, or +luminance and -chromatic) was presented in both intervals of a trial, and the chromatic test was presented in one. The chromatic pedestal component produces weak tilts of the nominal luminance pedestal in the Weberian coordinates. Fig. 6 shows that the dipper has now disappeared, since the curves are flat near the vertical midline. This indicates that the observer detects the chromatic test on the basis of an *approximately constant chromatic vector difference* between pedestal and pedestal-plus-test, thus demonstrating that the chromatic mechanism on the luminance pedestal acts approximately linearly. Wandell (1985) reported similar linear behavior of chromatic detection under different conditions. Linear detection (of a signal known exactly--Pelli, 1985) predicts that the psychometric function for chromatic detection on the luminance pedestal would have an exponent ~1 (log d' vs log test intensity), which we ascertained (Cole *et al.*, 1990). (This slope of 1 corresponds to a Weibull exponent of 1.25--Pelli, 1987.)

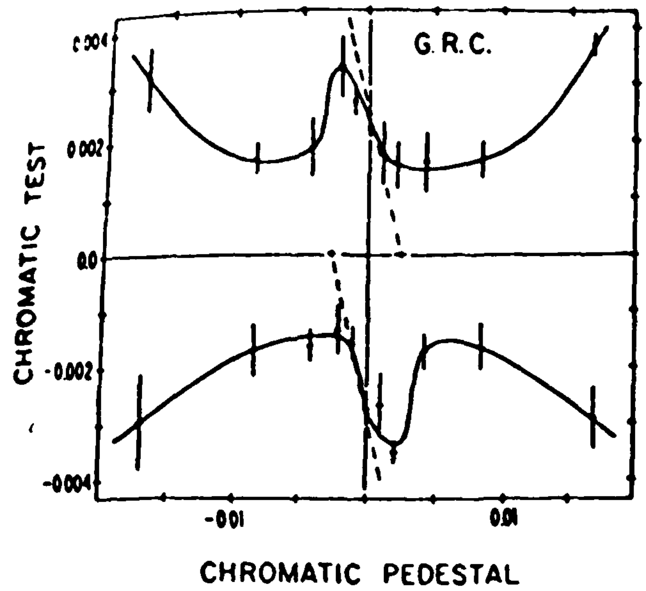

Fig. 5 Same as in Fig. 4, but the pedestal is now chromatic, and is either green (positive) or red (negative). The facilitation depends upon relative polarity, and the intense pedestals cause masking.

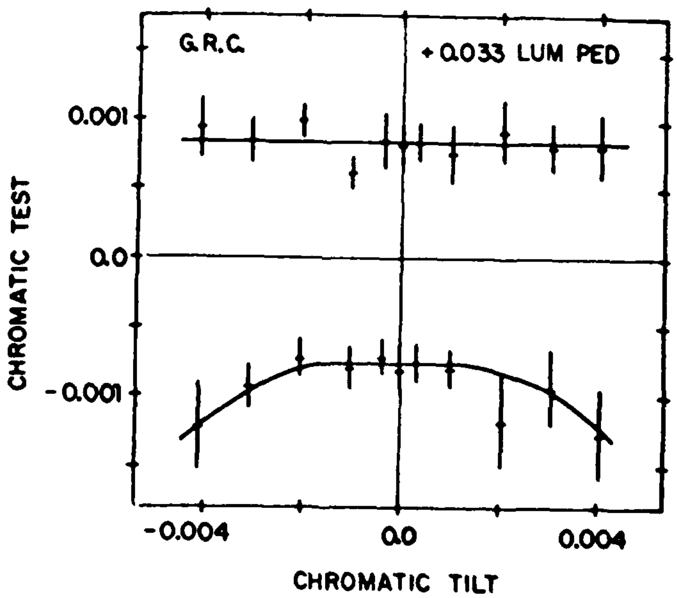

Fig. 6 Same as Fig. 5, but a luminance pedestal is presented along with the chromatic pedestal. The asymmetry in Fig. 5 has disappeared, showing linear detection.

A suprathreshold 1° luminance pedestal thus improves chromatic discrimination in two ways: (a) the pedestal produces facilitation of 2-3x; (b) with the luminance pedestal present, the observer is sensitive to an approximately constant chromatic difference between pedestal and pedestal-plus-test. The following illustrates these two effects. For observer GRC, the ±chromatic threshold measured on the uniform yellow field is equivalent to a calculated wavelength discrimination threshold of approx. ±0.16 nm relative to the field wavelength. With the facilitatory luminance pedestal, the observer can discriminate flashes in the two temporal intervals that differ from *each other* by a constant amount of less than one half this value (0.06 nm) or two flashes which each differ *from the field* by only 0.03 nm but in opposite directions.

Other findings are briefly listed (Cole et al.):

(1) Dichoptic test. There was no facilitation when the yellow adapting field was viewed by both eyes and the chromatic test and luminance pedestal were viewed by opposite eyes. This is puzzling, since our other results (described below) suggest that the facilitation occur at a high level in the visual system (presumably after V1, the first site of binocular combination). However the lack of binocular facilitation is consistent with most other color-contour interaction phenomena (like the

McCollough effect), which are largely monocular (Stromeyer, 1978).

For the remaining results, we revert to the original monoptic conditions.

(2) Annular ring pedestal. A thin luminance ring that just surrounded the chromatic test produced the same facilitation as the full 1° pedestal disc. Thus the facilitation seems to be edge-related, with the pedestal serving to demarcate two regions of different color: test and surround. This was examined by eliminating the surround.

(3) Eliminating surround. When the surround was removed, the luminance pedestal either had no effect on chromatic detection or it produced masking. The experiments of Nick and Larimer (1983) with blue tests on yellow pedestals, also showed that facilitation decreased and eventually disappeared as the surround was reduced in steps to the size of the coincident test and pedestal.

(4) Steady stimuli. Facilitation was still present but reduced in strength when the pedestal was steady rather than being flashed on with the test; the reduction could be a result of fading due to good fixation.

3. Time Course of Facilitation

We have examined the time course of facilitation using the 1° luminance pedestal and chromatic flash on the yellow field.

More than 100,000 forced-choice trials were collected (Eskew et al., 1989a). We measured the time course of facilitation, in order to model real-time contour extraction. The pedestals and tests were of various durations, and the luminance pedestal was temporally displaced from the chromatic test. Selected results for a 30 ms pedestal with tests of 30, 200, and 600 ms are shown in Fig. 7a,b,c. The box on the abscissa represents the chromatic test: negative SOAs indicate that the luminance pedestal was turned on before the onset of the chromatic test, whereas positive SOAs indicate that pedestal onset followed test onset. The results may be summarized as follows: (1) There is a narrow temporal window within which facilitation occurs, beginning ~100 ms prior to test onset and ending near test offset. (2) The maximal facilitation is a constant factor for each observer. Thus, a 30 ms chromatic test has a higher threshold than a 200 ms one, but the pedestal reduces threshold by about the same factor in each case. Our observers differ in their thresholds for the test on the uniform field, but differ very little in their facilitated thresholds. (3) For a brief 30 ms test, maximum facilitation occurs when a 30 ms pedestal is placed about 15 ms prior to test onset. (The fact that the luminance system is faster than the chromatic one might suggest that the maximum facilitation should come after test onset; our surprising result is accounted for by our model). (4) When the

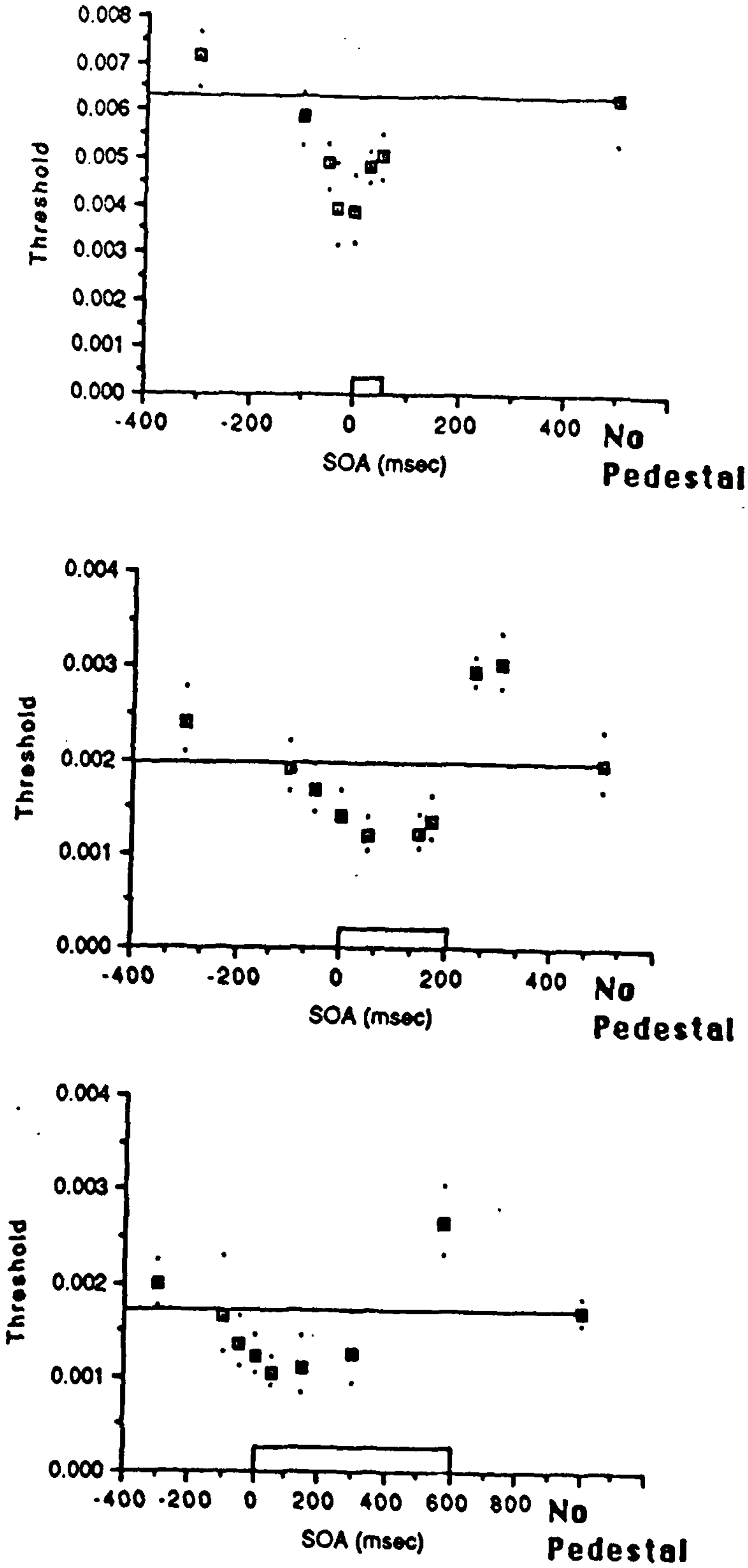

Fig. 7 Chromatic detection thresholds (dots show confidence intervals) as a function of the temporal displacement of a 30 ms luminance pedestal. The box on the abscissa represents the chromatic tests, which were 30, 200, or 600 ms in duration. The right-most point gives the unfacilitated threshold. Facilitation only occurs in a narrow window surrounding test occurrence; otherwise, there is masking.

pedestal follows test offset, or precedes test onset by more than 100 ms, there is masking; the offset masking is often accompanied by a color complimentary to the test (e.g. a subthreshold red test may be detected by the greenish appearance of the pedestal which follows the test). (5) The perception of test and pedestal as one event in time is necessary, but not sufficient, for facilitation to occur: at long positive SOAs (late pedestal), the test and pedestal appear to be simultaneous, but there is masking.

A quantitative model of the time course of facilitation is nearly complete. Using our estimates of the chromatic impulse response function (see below) and published estimates of the luminance impulse response function, we conclude that 15 to 25 ms are required for the mechanism underlying the facilitation to operate. The 15-25 ms are needed to generate a contour that segments the image into two regions and compare them--thus maximal facilitation occurs when the pedestal precedes the brief chromatic test.

4. Detection Uncertainty

A major effort during the past year has been made to test a class of explanations for the facilitation of chromatic detection by luminance contours: uncertainty reduction. Pelli's (1985) model of detection uncertainty shows that if an observer is uncertain as to the time or place of presentation of a stimulus, the threshold and psychometric slope for detecting that stimulus is elevated, when measured using 2AFC. A reduction in uncertainty, as might be produced by luminance contours demarcating the test region, reduces threshold and pyschometric slope, and seems consistent with the subjective experience of our observers (Fig. 2). Pelli's model makes two predictions: (a) when a Yes/No psychophysical procedure is used rather than 2AFC, the facilitation should disapear if the observer's criterion is held constant and the data are corrected for guessing; (b) the slope of the receiver operating characteristic (ROC), which is the ratio of the standard deviations of the noise and signal-plus-noise distributions (Nachmias, 1972), should be less than 1.0 without the luminance contour and closer to 1.0 with it. Both of these predictions are a consequence of the fact that uncertainty's only effects are to increase the mean and decrease the standard deviation of the noise distribution, causing more false alarms (and "spurious hits") in detection.

We have now completed an extensive quantitative test of these predictions (Eskew et al., 1989C, attached), by measuring psychometric functions (for Yes/No and 2AFC) and ROCs. Fig. 8 shows psychometric functions from two observers, obtained with the two methods. The same facilitation of threshold and psychometric function slope was obtained with 2AFC and Yes/No methods, even after data from the latter were corrected for guessing (which factors out the effects of uncertainty). Fig. 9 shows ROCs from three different observers; these ROCs had a slope of about 0.75 both with and without the luminance pedestal, on average. Neither result is consistent with Pelli's (1985) model, or with other models of uncertainty. The essence of the uncertainty reduction hypothesis is that there is a population of independent detectors and the luminance contour acts to select a subset of that population to be used in the detection task. The properties of the detectors--their spatial extents, for instance--are fixed throughout. Our rejection of this hypothesis implies that the contour may act to alter the properties of the detectors, rather than simply select among them.

5. Contour Variations for Facilitation

We have begun a series of experiments to explore the effects of spatial variations in the luminance pedestal.

(a) Effects of pedestal area

Fig. 10 shows detection of a 1° chromatic flash on concentric suprathreshold luminance pedestals (disks) of various diameters. The dashed line, for pedestals larger than the test, shows that the data fit the prediction of uniform areal integration of chromatic flux over the pedestal area. The facilitation falls to half when the pedestal is enlarged so that its contour falls a full 15-20' from the edge of the chromatic test.

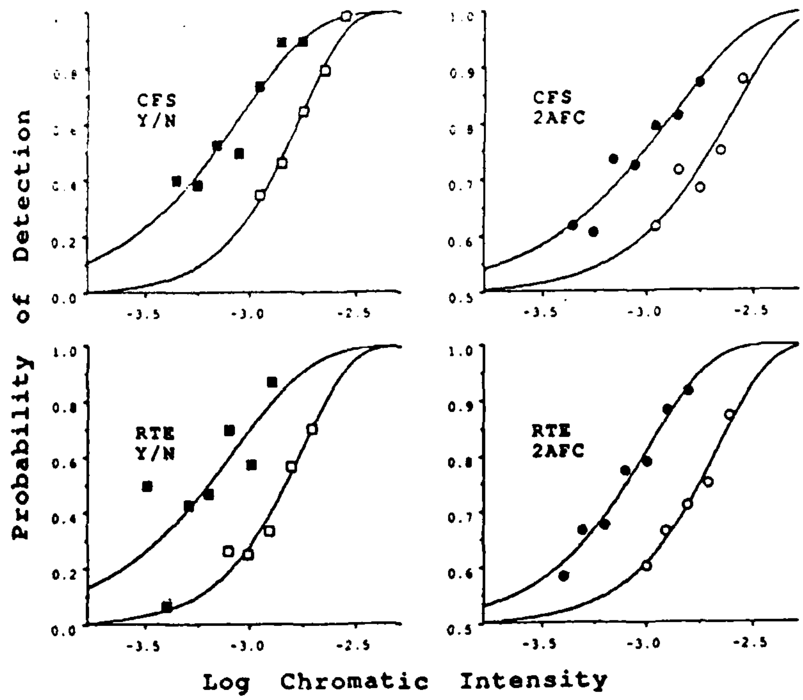

Fig. 8 Chromatic psychometric functions measured with Yes/No (data corrected for guessing) and 2AFC methods. Filled symbols indicate the luminance pedestal condition. Facilitation does not disappear when the data are corrected for guessing.

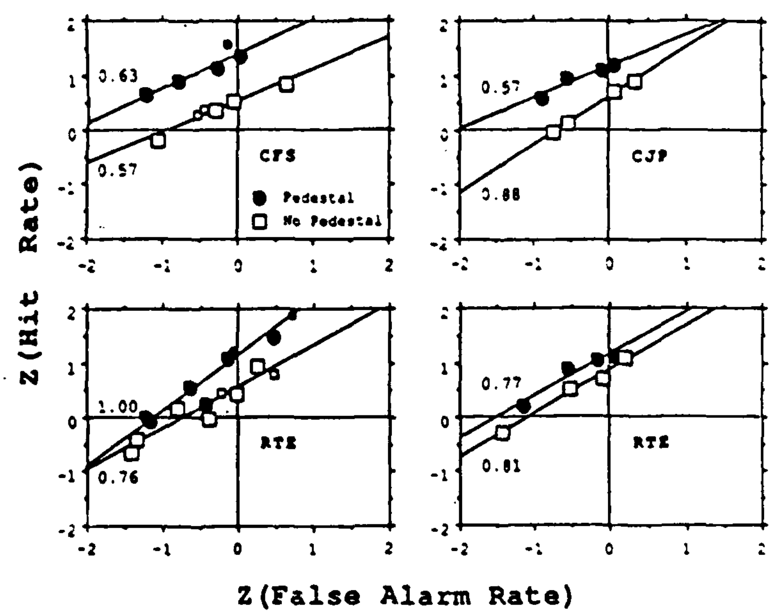

Fig. 9 Receiver operating characteristics for chromatic detection, measured with (filled symbols) and without (open symbols) a luminance pedestal. The number in each panel gives the slope of the ROC. The pedestal did not significantly alter the slope, on average, showing that the pedestal does not alter the observer's detection uncertainty.

(b) Effects of ring location

Fig. 11 shows the effect of spatially displacing the luminance ring relative to the chromatic disk. The results, like those in Figure 10, are roughly consistent a model in which the visual system integrates within the demarcated region and makes a comparison with the surrounding area, causing a decline in facilitation with displacement or changes in size. Facilitation is nearly eliminated when the ring is displaced over far enough to bisect the test. Our result contrasts with the result of Switkes et al. (1988), who found that the facilitating effect of a luminance grating on the detection of a chromatic grating was independent of relative phase.

(c) Effect of partial ring location

Fig. 12 shows the result of using only a section (90 deg) of the luminance ring as a pedestal, and flashing it at various displacements relative to the edge of the chromatic test. When the arc is aligned with the edge of the test (0 displacement), threshold is reduced by about half as much as it is for a full, aligned ring (see next paragraph). Remarkably, the four observers show excellent agreement in the absolute value of threshold under this condition just as they do with the full disk pedestal. Facilitation falls off rapidly as the arc is moved away from the test (negative displacements). Interestingly, the threshold falls off much less as the arc is displaced inside the test area (for

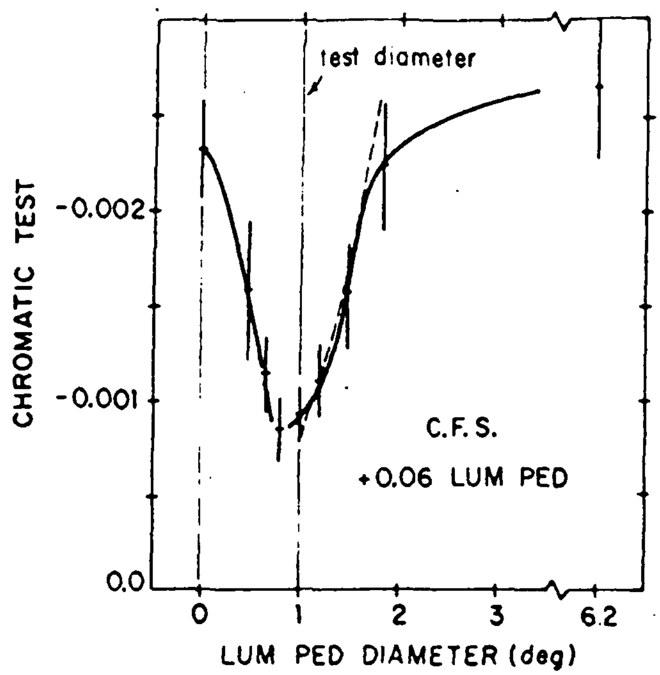

Fig. 10 Chromatic detection threshold as a function of the diameter of a luminance pedestal (a disk). Facilitation is maximal when the size of test and pedestal match, and declines otherwise.

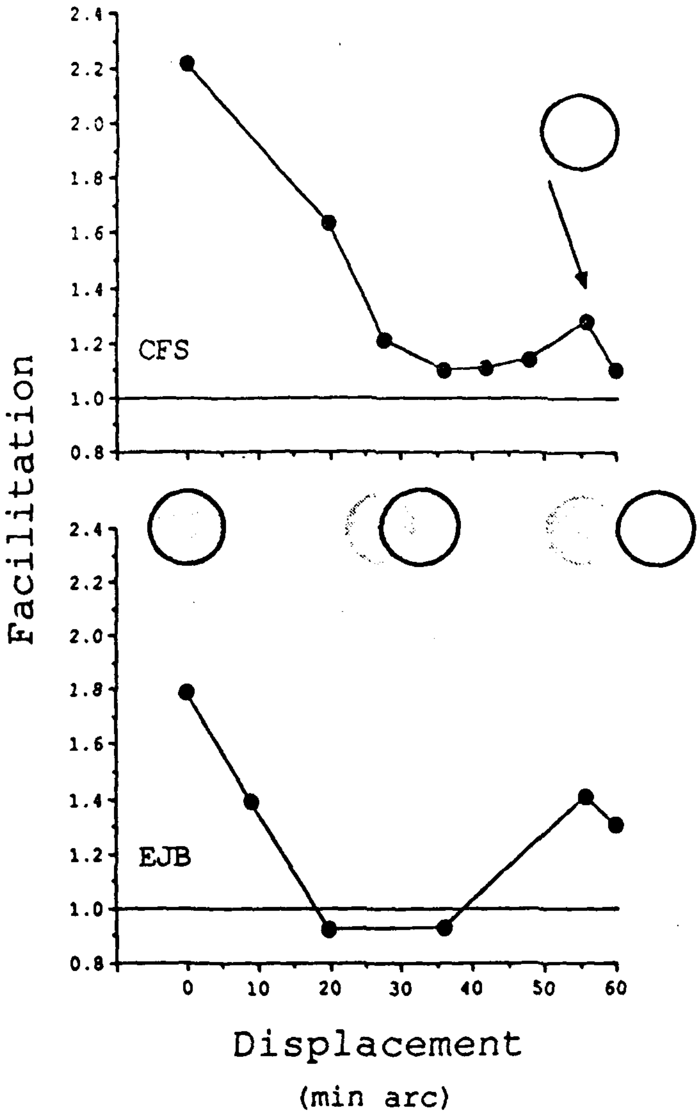

Fig. 11 Amount of facilitation as a function of the displacement of a luminance ring pedestal. When the ring bisects the test, there is little or no facilitation.

three of four observers). Observers often saw a blob of color, nestled within the arc, as the arc was flashed within the test area. The fact that a (curved) line segment placed within the test region can facilitate chromatic detection poses a challenge to all potential models of the facilitatory process, since the line does not demarcate two regions which differ in color. Instead, the line may raise sensitivity (locally) in some way which is not yet understood. Experiments are currently underway to manipulate the length of lines placed within the test, in order to better understand this crucial phenomenon. The model structure of Grossberg and his colleagues provides one possible means of accounting for these data (see Section 6, below).

(d) Effect of ring arc length

Fig. 13 shows the effect of varying the arc length of a part of a ring which is aligned with the edge of the test, and therefore partially demarcates it from its surround. Facilitation is small but measurable even for short arc lengths; it then increases only slightly out to 90 deg of arc, and by 180 deg the be two distinct mechanisms: one operates on short contours (≤90 deg) and produces 30-40% of maximum facilitation, and the other (≥120 deg) operates on a bounded region (not necessarily a physically closed boundary) and produces 100% facilitaton; presumably it is this latter mechanism which causes the fall-off seen in Fig. 11. It is not clear why the smaller mechanism seems

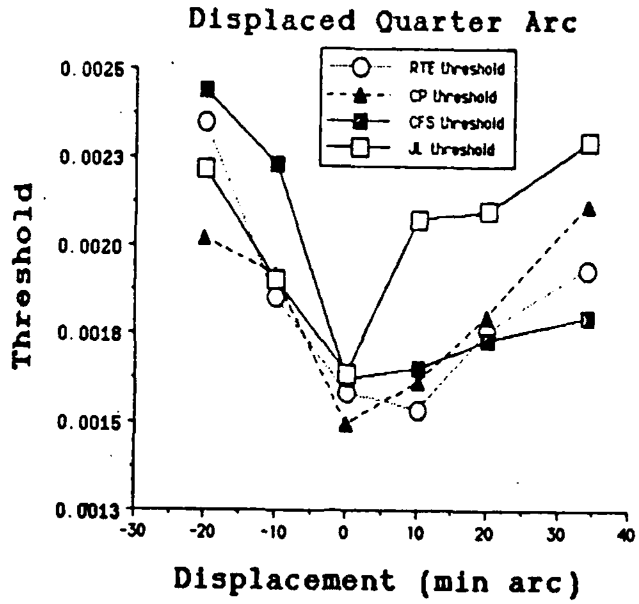

Fig. 12 Chromatic detection threshold as a function of the displacement of a 90 deg segment of the luminance ring. For three observers threshold falls off less as the contour is put inside the test (positive displacement) than it does outside the test (negative displacement).

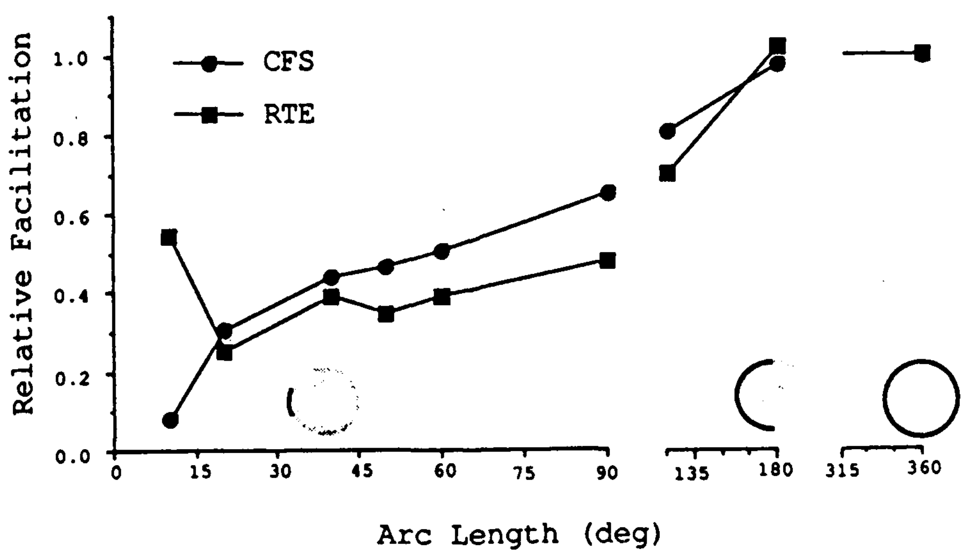

Fig. 13 Relative chromatic facilitation as a function of the arc length of a luminance ring pedestal, normalized such that the 360 deg ring produces a facilitation of 1.0. Short arcs produce 30-40% of the full effect, and facilitation is complete by 180 deg.

to have little effect when the full ring is displaced mid-way over the test (Fig. 11); it perhaps suggests that the two mechanisms are not independent.

A simple analysis shows that if each small segment of contour invoked an independent facilitatory mechanism, then probability summation among the small scale mechanisms would produce far more facilitation than we actually observe when the full ring is used. In this sense the facilitation is "sub-optimal". This suboptimality might occur because the small mechanisms interact so as to produce a unified percept -- above threshold -- rather than the lowest possible detection threshold.

6. Grossberg's Model

Grossberg and colleagues (Grossberg, 1987a,b; Grossberg and Mingolla, 1985; Grossberg and Todorovic, 1988) proposed an elaborate neural network model for suprathreshold phenomena which can be related to our proposed experiments. The model postulates two distinct subsystems: (1) A 'feature contour' system, which contains a two-dimensional syncytium or network of tightly-coupled cells whose activity represents brightness and color. Activity spreads between cells of this network via diffusion, producing a kind of visual filling-in. (2) A 'boundary contour' system, which provides local contour signals that alter the diffusion coefficients of the syncytium. The boundary contour signals produce barriers which impede diffusion of signals in the feature contour system. A key feature of this boundary contour system is that it can perceptually complete physically incomplete contours (see below).

Grossberg's model is intended to account for suprathreshold phenomena; however, the model could be extended to explain our results, as follows. The 1° chromatic test at threshold may produce signals only in the feature contour system, accounting for the diffuse, 'blob-like' appearance of the test. The suprathreshold luminance pedestal may activate the boundary contour system and form a compartment in the syncytium, causing facilitation by limiting the chromatic diffusion.

The model (Grossberg, 1987b) also accounts for binocular interactions. The boundary contour system is binocular at a fairly early level in the model, and the filled-in percept occurs *binocularly*. Our experiments (Section 4), however, show no dichoptic facilitation of the chromatic test by the luminance pedestal, and thus the chromatic filling-in seems *monocular*.

Grossberg's model might account for the results with the displaced 90° arc (Fig. 12). As the arc is placed further outside the test, it has less effect in impeding diffusion of the color signal in the "feature contour" system. Fig. 12 suggests an effective diffusion length on the order of 10 min arc. When the arc is approximately centered within the test region (34 min displacement, Fig. 12) it should have little effect in impeding diffusive spreading of color (a straight centered line would have no effect, since the diffusion is radial). Thus to explain the substantial facilitations (shown for three of the four observers) on the right-hand side of Fig. 12 using the model, the other subsystem must be invoked. This "boundary-contour" system could complete an illusory boundary between the two ends of the arc and form a compartment, within which diffusion might be completely contained, leading to substantial facilitation.

Complete quantitative tests of Grossberg's model have yet to be performed, but data such as these clearly can provide an important test. Further applications of the Grossberg model, and variations of the model, to our data are in progress.

7. Chromatic Gap Effect

These experiments involve very different stimuli and methods (see attached reprint, Eskew, 1989). The stimulus was a small rectangular, equiluminant bipartite field (each half was 0.19° wide by 0.90° high). The left half was an isoluminant mixture of 551 and 410 nm (tritanopic metamers, discriminable only by S cones) or 551 and 648 nm (discriminable only by the red-green chromatic system). The right half was 551 nm. The observer used the method of adjustment to find the threshold difference between the two half-fields.

The basic gap effect of Boynton *et al.* (1977) was replicated: a narrow, dark gap placed between the two isoluminant half-fields improved chromatic discriminability of the half-fields. Surprisingly, this positive gap effect was maintained (for an S cone discrimination) even when the gap was filled with light isoluminant with the test fields. The gap could be filled either with white light or with red light. The latter gap was not seen by the S cones, thus suggesting that the positive gap effect can be produced by the interaction of two chromatic channels (an S cone pathway and red-green, M-L, pathway). The results are relevant to Gregory's hypothesis, that the luminance system provides the 'master' map, because this chromatic gap effect shows that chromatic contours can also prevent filling-in.

E. Chromatic Impulse Response

These experiments measured temporal properties of the red-green opponent channels in isolation (no interacting luminance contours). Stimuli were similar to those described above, but the luminance pedestal was not used.

Three lines of evidence suggest the chromatic temporal filter is weakly bandpass: (1) The complementary color percept mentioned above in connection with our SOA study (Section C3), which can be accounted by an impulse response with a negative lobe. (2) When a long (600 ms) chromatic test is used, and a brief luminance pedestal is placed at various SOAs during the test, the facilitated threshold rises slightly during the latter portion of the test; if the impulse response were monotonic, the facilitated threshold should reach an asymptote and not rise. (3) Our measurements with a two-pulse perturbation technique show that the chromatic impulse response function has a negative lobe. Two 11 ms chromatic flashes were separated in time, with the first fixed in amplitude and the second varied to find the threshold for the ensemble. Results for one observer are shown in Fig. 14: at separations greater than ~100 ms, there is inhibition between like-signed chromatic flashes and summation between opposite-signed flashes. Analytic impulse response functions have been fitted to these data using the probability summation model of Watson (1979).

F. S Cone Signals

Other empirical work performed under joint Air Force and NIH sponsorship includes the completion of a project to measure and model the phase lag of the short-wavelength, S, cones as they feed into luminance and chormatic mechanisms. It had been thought that S cones contribute exclusively to color, but we have demonstrated S cone input into chromatic and luminance pathways.

We briefly describe two principles that allowed us to separate better the mechanisms: (a) Luminance flicker discrimination (below) and detection of motion may best reveal the S cone input to the luminance, Lum, mechanism. (b) The phase lag of the S cone signal into Lum is much greater than for S into red-green (RG) and blue-yellow (BY), mechanisms, while the lag appears

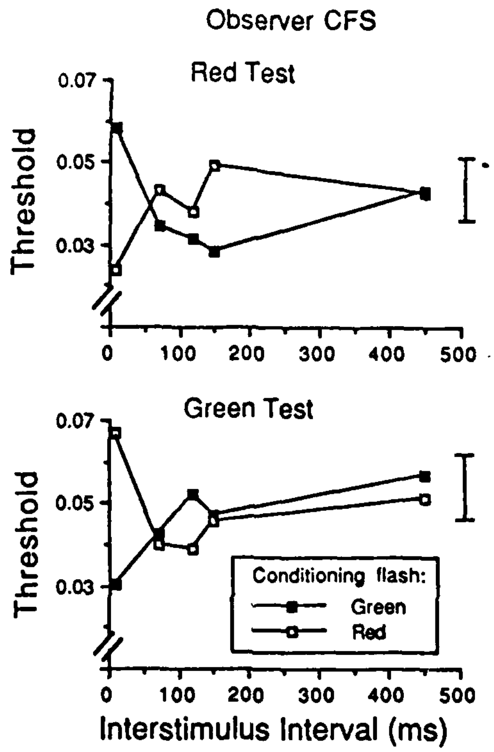

Fig. 14 Threshold for detecting an ensemble of two 11 ms equiluminant chromatic flashes, as a function of the time interval between the flashes and their chromatic polarity. Near 150 ms ISI, it is harder to detect a pair of same-colored flashes than a pair of oppositely-colored flashes, showing that the chromatic impulse response function has a negative lobe (i.e., is temporally bandpass).

similar for RG and BY. This differential phase lag allowed us to separate luminance and chromatic mechanisms.

1. **Contribution of S Cones to Motion and Luminance** Lee & Stromeyer (1989) investigated this topic with violet and orange stimuli (1 cpd gratings or uniform flicker) on an intense 559 nm field. Violet and orange stimuli stimulated essentially S and L respectively.

(a) S cone motion mechanism at detection threshold?

The moving 441 nm violet grating on the yellowish field (grating signalled by S cones) appeared as alternating yellow and white stripes; little motion was visible at threshold. In 2AFC we showed moving gratings had to be well suprathreshold for their direction to be seen; the threshold ratio of counterphase vs moving grating was low, as Watson et al. (1980) observed for luminance patterns detected by nondirectional mechanisms. Thus the most sensitive mechanism for detecting the patterns may be nondirectional, possibly a BY mechanism. When the moving grating was well suprathreshold, the yellow stripes often appeared still, while the whitish stripes moved veridically (as shown by velocity matching). The latter movement suggests there are less sensitive, motion mechanisms, described next.

(b) Luminance motion mechanism

The S and L cone signals were shown to feed into a common motion detector. We measured direction identification thresholds for the motion produced by a pair of orange and violet counterphase gratings flickered at the same rate and presented in spatial quadrature (90°) phase. Since neither grating alone had net left or right motion, the motion of the pair results from the interaction of S and L signals. Thresholds were measured as a function of temporal phase of the two flickering gratings, and an analytic template was fitted to the data to determine the relative S to L cone lag. The lag varied with S cone light adaptation: at 8.4 log quanta.deg^{-2}.sec^{-1} (re 441 nm) the S lag was ~180° at 12 Hz. Measurements extrapolated to 0 Hz showed the S cone signal is inverted (has negative sign), confirming Stockman et al. (1987) for luminance flicker.

Threshold summation was then measured for *direction identification* of a pair of violet and orange gratings moving at the same velocity but with different spatial phase offsets. The above temporal templates predicted the degree to which the violet grating had to be spatially advanced relative to the orange to compensate for the S lag. At the trough of each curve in Fig 15 the two patterns linearly summate at threshold and at the peak they cancel. The summation demonstrates that the *most sensitive* motion detectors have an S cone input. At 9 Hz the contrast sensitivity is *very high* for the orange grating (~0.5% contrast threshold); we thus conclude that the motion is likely detected by a sensitive luminance mechanism, which has an S cone input. We also measured the S cone lag for luminance discrimination of uniform flicker. Virtually the same S cone lag was found for motion or luminance flicker.

2. S Cone Lag for Chromatic Mechanism (described in the enclosed manuscript, Stromeyer et al., 1989).

The S lag is much less for chromatic discrimination than for the above luminance tasks. For the RG mechanism, red-green eqiluminant flicker (a -45° vector in the $\Delta L/L, \Delta M/M$ plane) was presented on the 559 nm adapting field. A phase discrimination paradigm was employed. The red-green flicker was identical in both intervals of a 2AFC trial. Violet flicker was added at temporal phase ϕ (relative to red) in one interval and added at ϕ-180° with the same amplitude in the other interval. The violet flicker was varied in amplitude between trials to measure the threshold for discriminating the two intervals as a function of ϕ. A template was fitted to the results; the symmetry axis gives the S cone lag for the RG mechanism. For the BY mechanism the red and green antiphase flickering components were shifted inphase and adjusted to form a +45° vector in the $\Delta L/L$, $\Delta M/M$ plane (the flicker is now luminance or yellow on the whitish adapting field). This flicker was combined with the violet flicker, as before. The observer based his discrimination on the apparent 'luminance' difference between the two intervals *or* on the 'yellow' chromatic difference. Fig 16 shows templates for these two tasks measured at

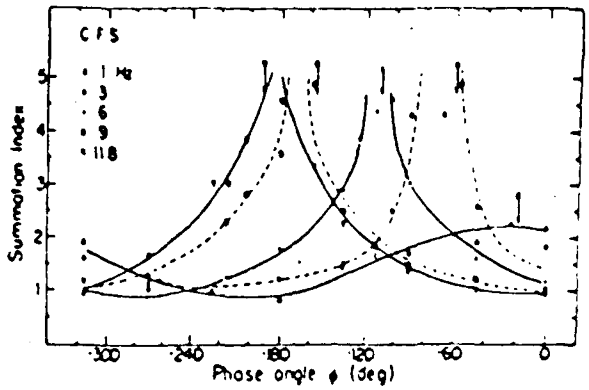

Fig. 15 Degree of threshold summation betwen violet and orange moving gratings, as a function of relative spatial phase. There is an S cone input to motion detection.

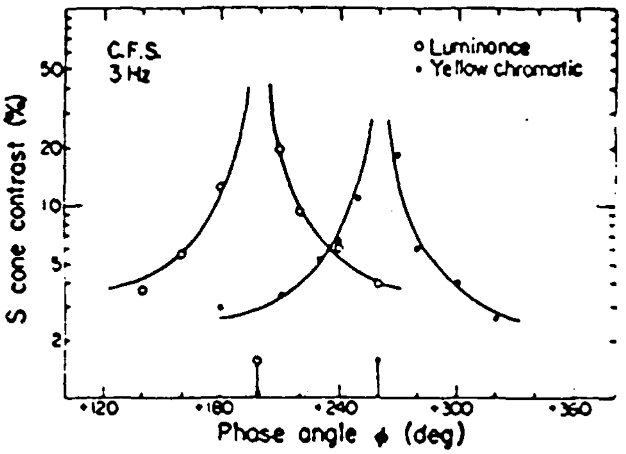

Fig. 16 Threshold amount of S cone flicker added to L-M flicker at phases ϕ and ϕ-180° in two temporal intervals. The observer discriminated the two intervals on the basis of their luminance or their color difference. The fitted templates show S cone inputs into two distinct mechanisms.

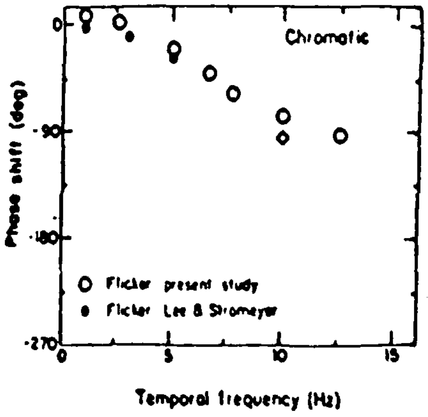

Fig. 17 Relative phase of the S cone input to red-green flicker as a function of temporal frequency, derived from data like those plotted in Fig. 16.

3 Hz. (Similar results for a second observer yielded peaks of 189° and 268°.) Although highly subjective, the task yields reliable quantitative results. The difference between the peaks is striking, demonstrating that the S cone lag for the putative BY mechanism is only ~10° at 3 Hz while the lag for Lum is ~80°. At the peak of the luminance template the S and M+L signals are in *quadrature* (90°) phase for Lum but approx *inphase* or in *antiphase* for BY. This large phase difference can be used to separate the BY and Lum mechanism. The open circles in Fig 17 show the S cone lag for RG; at ~3 Hz the lag is ~10°. Thus at 3 Hz the S cone lag for RG and BY seems very similar, and much less than the S cone lag for Lum. The large lag for Lum is documented in Lee & Stromeyer (1989).

G. Publications and Publications in Progress

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